

A Study of the Bionomy of the Spanish Pollen Wasp *Ceramius hispanicus* Dusmet (Hymenoptera, Vespidae, Masarinae): Nesting, Mating, and Flower Associations

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Abstract.—Data about the bionomy of the Spanish pollen wasp species *Ceramius hispanicus* Dusmet are presented for the first time. Following the concept of Gess and Gess (1988) *C. hispanicus* can be characterized by the following ethological elements: a. Nest excavated in non-friable soil; b. Burrow surmounted by a turret from earth extracted from within the burrow; c. Nest possibly annual; d. Nest with relatively short main shaft, main shaft vertical to sub-vertical, with an expansion at the bottom of the shaft; e. Main shaft not terminated by a cell; f. Secondary shafts absent; g. Cells sub-horizontal, in a group to one side, all at different depths; h. A constructed mud-cell within an excavated-cell, formed from earth excavated within the burrow; i. Main forage plants are representatives of Cistaceae, Primulaceae, Lamiaceae, and Fabaceae. The entrance turret of the nest is unique in that it is reduced to three distally converging processes. During nest excavation the females perform pellet dropping flights and use a defined pellet-dropping area. Water is used to soften the soil. Females alight on the edge of a water source to collect water. Cell construction rate during this investigation was about 0.5 cells per day. Analysis of brood cell contents revealed *Ceramius hispanicus* to be polylectic. Cells were found to be provisioned with pollen originating from six different plant families. The most important pollen sources were *Helianthemum* (Cistaceae), *Coris* (Primulaceae), several species of Lamiaceae, and *Lotus* (Fabaceae). Pollen grains of the same plant taxa were found in crop and rectum of both male and female wasps. Males patrol and perch at water and to a lesser extent at flowers. Pairings were frequently observed at water. The daily period of activity lasted about 10 hours. Activity of males at water was high in the morning and declined during the day, while female activity increased towards the afternoon.

The genus *Ceramius* shows a disjunct distribution with six species-groups occurring in the Afrotropical Region and two species-groups in the Palaearctic (Richards 1962, Gess 1992). For the Afrotropical taxa it has been shown that there are distinct differences between the species-groups in regard to nest construction and flower association (Gess 1996, Gess and Gess 1980, 1986, 1988, 1990). By contrast, the bionomy of the Palaearctic species is insufficiently known (cf. Gess 1996) to make it possible at present to draw conclusions about the evolution of life history traits

within the whole genus. For the Palaearctic Region comprehensive information is only available for *Ceramius tuberculifer* Saussure (Ferton 1901, Giraud 1863, 1871, Mauss 1996a). The knowledge of the bionomy of the remaining 13 species is very poor (cf. Fonscolombe 1835, Mauss 1998, Richards 1963), bionomical data concerning *Ceramius hispanicus* Dusmet are completely lacking. Like *Ceramius tuberculifer*, *C. hispanicus* belongs to *Ceramius* species-group 7 of Richards (cf. Mauss 1996b). However, these species are not very closely related, i.e. *C. hispanicus* is not a mem-

ber of the *C. lusitanicus*-complex (Mauss 1996b). Biogeographically *C. hispanicus* seems to be restricted to Central, Eastern and Southern Spain (cf. Ceballos 1956: 342, Richards 1962: 107, Mauss unpubl.).

Data concerning habitat, nest architecture, flower visiting, male activity and mating of *C. hispanicus* are presented here for the first time and are compared with ethological accounts for other species of *Ceramius*.

METHODS

Investigations were carried out from 19 to 26 June 1998. Weather conditions were good throughout the whole period. Maximum air temperatures were circa 30 °C. Sunrise took place at 4h24, sun-transit at 11h56 and sunset at 19h28 (Bien in lit.). Time used is Greenwich Time. Observations were made with the aid of close-up binoculars (Eschenbach Binoskop) and documented using a 35 mm camera with a 100 mm lens (scale up to 1:1) or a 300 mm lens.

Activity of males and females at water was measured on 21 June (from 8h30 to 18h30) and 24 June (from 7h00 to 18h30). A rectangular sample area of 2m × 1m was marked out with a string. The area was completely shaded by the ridge of a mountain after 17h30. Accuracy of counting was improved by use of mechanical hand-counters. Every half hour a measuring cycle lasting 20 minutes was carried out following the sequence:

1. Activity of females measured by counting the number of females sitting on the ground of the sample area every 30 s during a period of 300 s, leading to 10 counts per period.

2. Activity of males measured by counting crossings of the string into the sample area (category "males flying") during a period of 600 s and counting landings on a perch within the sample area (category "males perching").

3. Activity of females measured again during a period of 300s as described in 1.;

female activity per half hour is the sum of the 20 counts of a complete measuring cycle (category "females at water").

Copulations were counted during the complete 1200 s of the measuring cycle irrespective whether they occurred inside or outside of the sample area. A situation was rated as a "copulatory attempt" when at least a short struggle on the ground could be observed after a male approached a female and pounced on her.

Finally, two thermometers (precision: 0.5°C) were read one of which was situated 0.5 m above the ground in the shade within a juniper tree (T_{air}), the other one was placed on the wet ground with its point in the shadow of plants (T_{ground}). Short notes were made about the weather. Radiation conditions were noted applying the categories "cloudless" (sun not covered during the whole period), "hazy" (sun covered by hazy clouds at least for a short period, resulting in half shade) and "cloudy" (sun covered by clouds at least for a short period, resulting in shade). The observed frequencies of the measured behavioural categories were summed up for every hour. Then the proportion of activity for each hour to total activity for the day was calculated separately for each category and expressed as a percentage. For statistical analysis, a Chi square test was performed which was calculated by Abacus Concepts, StatView® Student for Macintosh. For 21 June the period from 8h30 to 12h30 was compared with the period from 12h30 to 16h30. For 24 June the period from 6h30 to 12h30 was compared with the period from 12h30 to 18h30. For each category the observed frequencies were tested against the expected equal distribution.

For nest excavation on 26 June the shaft of each nest was completely filled with Maizena® (fine maize flour) which was injected with a squeezing bottle. Nests were carefully excavated afterwards. Measurements were taken by use of small strips of graph paper, orientation of the cells was

measured with a bearing-compass. All nest cells were collected and stored in a refrigerator for three days. Afterwards, all cells were measured (external maximal dimensions) using a stereo-microscope (Wild M3) with a calibrated ocular-micrometer; then they were opened and the contents were recorded.

Flowering plants in the neighbourhood of the nesting site were collected and preserved both dried and in 70% ethanol. They are named according to Tutin et al. (1964–1980). Pollen samples from the nest and the alimentary tract of imagines fixed in Bouin's solution were prepared using the method outlined by Westrich and Schmidt (1986). The different pollen types were ascertained under a light microscope at a magnification of 400 \times or 1000 \times and determined to the family or genus level with the aid of a reference collection consisting of pollen samples of 500 mainly Mediterranean plant species including those growing at the nesting site. Exact knowledge of the plant species flowering at the study site during nest provisioning in some cases allowed pollen determination down to species level. The percentage of the different pollen types per brood cell was estimated by counting 50 grains at each of 30 loci distributed randomly over the cover slip. For each gut sample between 100 and 250 pollen grains were counted.

RESULTS

Description of the habitat.—A large population of *Ceramius hispanicus* was localized in the Barranco de Zorita (GPS: 01°26.402' W 40°27.334' N), a small valley in the Sierra de Albarracín about 6 km north of Albarracín in Teruel province, situated on the north-east slope of the Vallejo Largo at an altitude of 1200 m. The narrow, steeper part of the valley was orientated from the east-south-east (downstream) to the west-north-west (upstream); at the upper end it got wider, sloped only gently and changed its direc-

tion towards the southwest. A water trough which was supplied by a perpetual spring non-seasonally was situated at the upstream end of the narrow part of the valley. The water ran away from the trough into a little stream (Fig. 1) that dried out after about 100 m. Further downstream a few puddles remained at first but they dried out during the observation period. Two small ponds were situated about 100 m upstream of the trough, the border of which was completely overgrown with rushes (*Juncus* sp., Juncaceae). The whole area was covered by sparse montane forest, on calcareous soil, dominated by trees and shrubs of different junipers (*Juniperus* sp., Cupressaceae) (cf. Polunin and Smythies 1973) forming a Junipereto hemisphaerico-thuriferae sigmentum (Rivas-Martínez 1986). The ground cover was about 70% in the valley but decreased markedly uphill where it became more rocky and much drier (Fig. 1). The following plant species were in flower: the Lamiaceae *Nepeta nepetella* L., *Marrubium supinum* L., *Sideritis spinosa* Lam. and *Thymus zygis* L., the Cistaceae *Helianthemum apenninum* (L.) Mill. and *H. cinereum* (Cav.) Pers., the Fabaceae *Lotus corniculatus* L., *Coronilla minima* L. and species of *Ononis*, *Hippocrepis*, *Onobrychis*, *Medicago* and *Vicia*, the Primulaceae *Coris monspeliensis* L., the Asteraceae *Anacylus clavatus* Pers. and *Achillea* sp., the Resedaceae *Reseda lutea* L., the Boraginaceae *Echium vulgare* L., the Rosaceae *Potentilla reptans* L. and unidentified species of Brassicaceae, Cichorioideae, Convolvulaceae and Crassulaceae. The area was grazed by sheep and goats. A small cornfield adjoined in the upper, widened part of the valley.

Nest site.—An aggregation of five nests was located on a bank of hard, clayey soil mixed with some gravel. The bank was about 20 m long, 2.5 m wide and rose above the adjacent terrace by 0.4 m. It was situated about 50 m upstream of the ponds and ran from the southwest to the

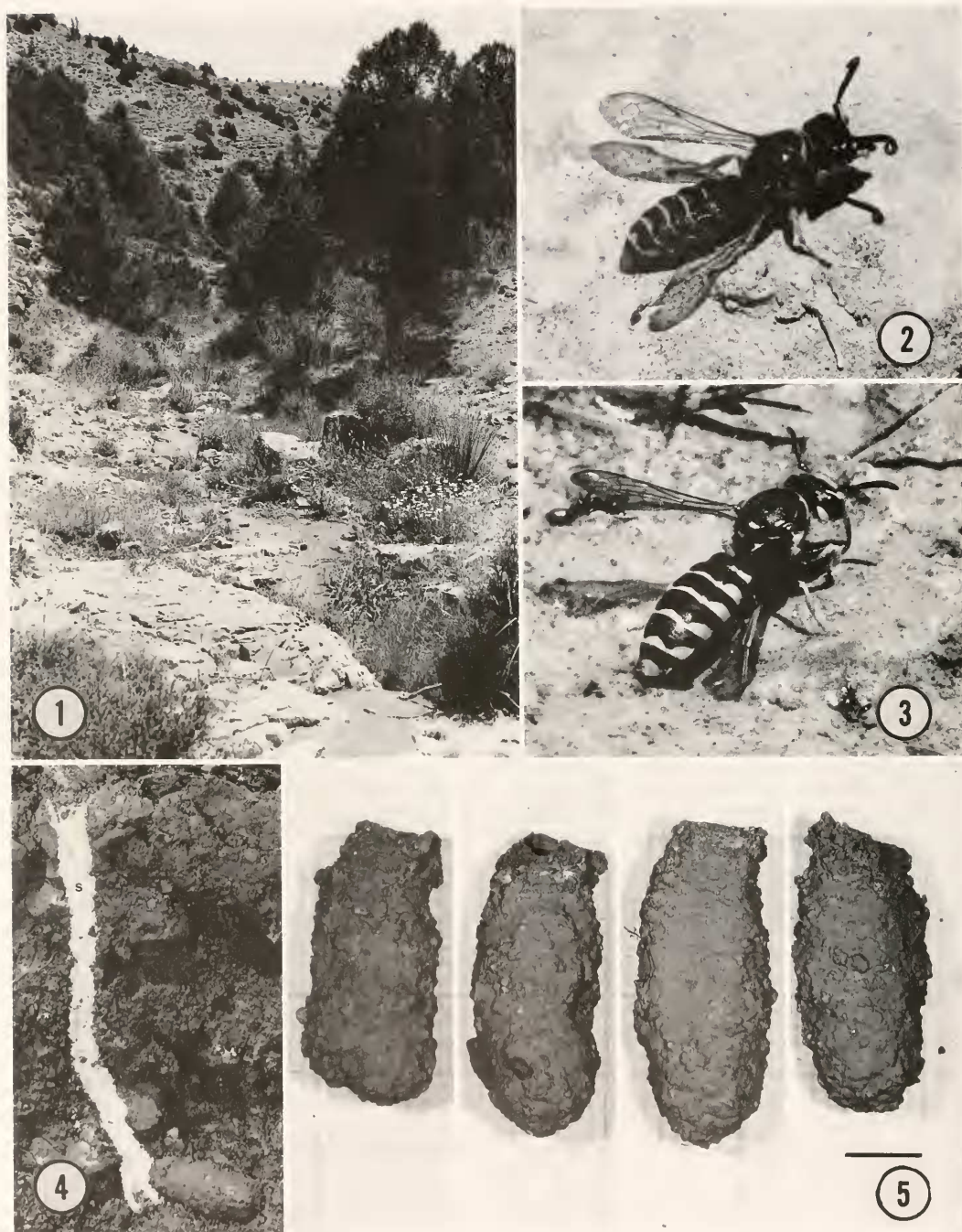


Fig. 1-5. 1, Habitat of *Ceramius hispanicus* at Barranco de Zorita (Prov. Teruel, Spain) covered by sparse montane forest dominated by different junipers. Males patrolled along the stream in the centre where females collected water. 2, Male of *Ceramius hispanicus* perching on a stone close to the water (glossa visible between slightly opened mandibles). 3, Female of *Ceramius hispanicus* standing on the wet ground at the stream during water uptake (note extended glossa). 4, Nest No. 4 of *Ceramius hispanicus* after excavation on 26 June, 1998 (turret removed, shaft filled with Maizena®; s = main shaft; c = constructed mud cell). 5, Constructed mud cells of nest No. 3 of *Ceramius hispanicus* on 29 June, 1998 (length of scale bar 5 mm).



Fig. 6–10. 6, *Ceramius hispanicus* female during nest excavation. The female had backed out of the entrance with the soil-pellet held in her mandibles and was about to turn round and start the pellet discard flight. The nest entrance is surmounted by three elongated, distally converging processes (= p; third process mainly hidden by the middle one) (see also Fig. 11). 7, Female of *Ceramius hispanicus* initiating the turret at the entrance of the main shaft (mud pellet supported by mid-legs on the outside). 8, Female of *Ceramius hispanicus* placing a mud pellet on the distal end of one of the processes of the turret. 9, Copulation of *Ceramius hispanicus*, male and female grappling on the ground. 10, Copulation of *Ceramius hispanicus*; male still connected to the female by its genitalia after it had lost its hold on the thorax of the female that had tried to escape. The situation lasted for about 180 s.

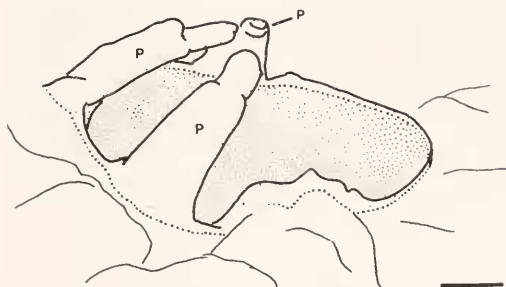


Fig. 11. Schematic representation of the nest entrance of *Ceramius hispanicus* (see also Fig. 6) (weakly dotted area = parts of the nest entrance which are made out of mud by the female; p = elongated, distally converging processes probably homologous with the turret; length of scale bar 1 mm).

northeast, gently sloping towards the latter. The nesting area measured about 2 m², its ground cover was 40–50%. The minimum distances between the nests varied from 0.4 to 1.2 m (median 0.7 m). Four nests were situated on the face exposed to the south-east and one was on top of the bank.

Nest architecture.—All nest entrances were to some extent hidden under leaves of plants. The entrance was surmounted by a low turret which was built of mud pellets cemented together. It consisted of a short basal ring which continued into the lining of the shaft towards the base. Distally, three elongated, converging, column-like processes arose obliquely from the basal ring (Figs 6, 11). The processes were about 3 mm long and were situated around that half of the entrance which was situated above the outside bend of the oblique outset of the shaft forming a three-pronged hood. Basally the processes were separated from each other by gaps of ca. 1 mm.

The shaft ran obliquely downwards at an angle of ca. 45° for the first 2–3 mm (Fig. 12). Below this it continued downwards more or less vertically for 40–60 mm, except in nest No. 2 in which the shaft descended obliquely to avoid stones (Fig. 12). This section of the shaft was 5–6 mm in diameter. The remaining part of

the shaft was obliquely or vertically orientated and was not terminated by a cell. It widened to 9–10 mm in diameter in the region of the brood cells which lay horizontally to sub-horizontally and radiated out from the main shaft. Secondary shafts were lacking so that the cell openings were directly integrated into the wall of the shaft. The constructed mud cells could be easily separated from the adhering soil (Fig. 4). The cells were elongate, more or less straight and noticeably wider at mid-length than before and after it; the inner end was markedly rounded (Fig. 5). Their outer surface was irregular but more or less homogenous (Fig. 5); the inner surface was smooth but dull. Measurements of each cell and details of its contents are listed in Table 1. The cell provision was a firm and relatively dry pollen and nectar loaf which did not adhere to the wall.

Nest-building behaviour.—Initiation of a nest by a female was observed three times. The females were flying slowly low over the ground. They interrupted their flight several times to alight on the ground which in some instances they scratched with their mandibles. At the future site of its nest, each female flew up from the ground and performed a circular orientation flight, the diameter of which was about 1m. Then the female alighted on the same spot again and directly started excavation.

Excavation was initiated by softening the soil with a liquid which was apparently regurgitated. A pellet of mud was formed by the mandibles; scratching movements of the fore- and mid-legs were performed in addition. When a pellet had attained about half the size of the head the female flew up with the pellet held between her mandibles. She flew very rapidly about 0.1 m above the ground towards an area situated between 0.3 to 0.7 m away from the nest in the immediate vicinity of a plant. At the end she hovered for a short moment, dipped down a few centimetres while dropping the pellet, re-

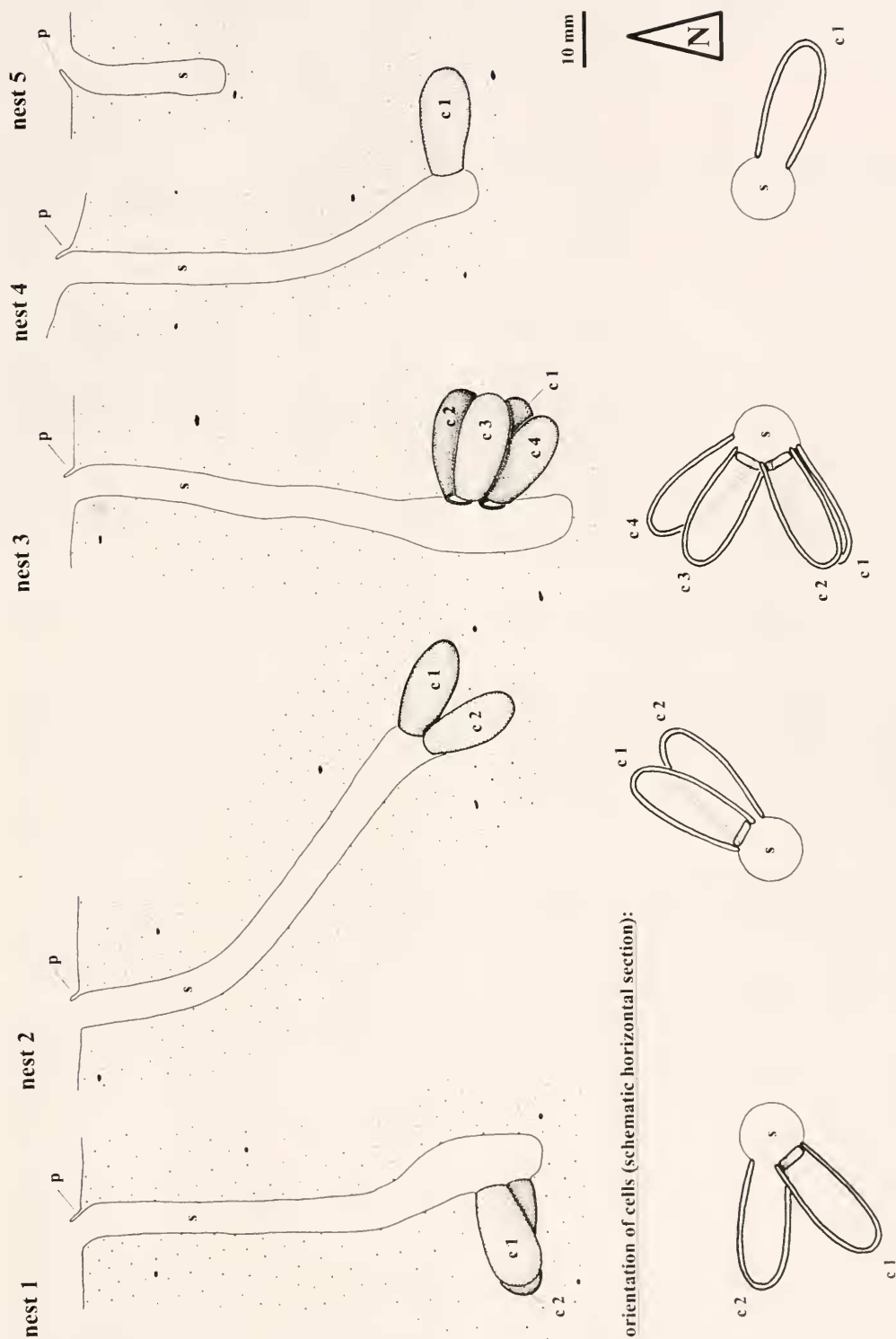


Fig. 12. Vertical plans of five nests of *Ceramius hispanicus* and plan views of the brood-cell arrangement (s = main shaft; c = constructed mud cell; p = distally converging median process of the turret; for further information see Table 1).

Table 1. Details pertaining to the five nests of *Ceramius hispanicus* excavated on 26 June, 1998 at Barranco de Zorita (measurements of cells and investigation of cell content were made on 29 June, 1998).

Nest data				Details of cells							
Nest no.	Date of founding	Σ females	Σ cells	Cell no.	Orien-tation	Depth below the sur-face of the ground (mm)	Exter-nal length (mm)	Exter-nal width (mm)	Inner diamet-er of cell open-ing (mm)	Condition	Content
1	22.06. 11h25	1	2	1	230°	73	?	?	?	sealed	small larva on pollen loaf
2	22.06. 12h47	1	2	2	275°	77	19.4	8.4	4.0	open	egg underneath pollen loaf
				1	30°	58	22.4	8.6	4.1	sealed	small larva laterally at the bottom of pollen loaf
3	22.06. 13h45	1	4	2	50°	64	21.0	8.2	4.3	open	egg underneath pollen loaf
				1	245°	69	17.3	8.4	4.1	sealed	larger larva below the pollen loaf
				2	245°	63	20.4	8.8	3.8	sealed	small larva laterally at the bottom of pollen loaf
				3	300°	66	17.5	8.8	3.8	sealed	small larva laterally at the bottom of pollen loaf
4	23.06.	1	1	4	320°	72	19.8	8.2	3.8	open	egg ± laterally from pollen loaf
4	23.06.	1	1	1	110°	63	20.4	8.8	4.2	open	small larva laterally at the bottom of pollen loaf
5	26.06.	1	0								

turned to the previous flying height again and flew rapidly back to the nest-initial. The female repeated the whole sequence of pellet formation and pellet dropping several times, in which always the same

Table 2. Flower-visiting records for males and females of *Ceramius hispanicus* during 11 hours of observation on three days at Barranco de Zorita (the number of flowers visited per plant is not taken into account).

Plant taxon	Number of plants visited by	
	Males	Females
Lamiaceae		
<i>Nepeta nepetella</i>	5	
<i>Marrubium supinum</i>	4	7
<i>Sideritis spinosa</i>		1
<i>Thymus zygis</i>		1
Fabaceae		
<i>Lotus corniculatus</i>		7
Cistaceae		
<i>Helianthemum apenninum</i>		2
<i>Helianthemum cinereum</i>	1	
Asteraceae		
yellow <i>Cichorioideae</i> sp.	1	

area was used for pellet dropping. All females continued to use their individual pellet-dropping areas over the whole observation period until 26 June. Once it was observed that a stone which was obviously too heavy to be removed by a pellet dropping flight was carried away from the nest-initial on foot. Formation of a pellet took about 30 seconds. After a female had discarded three to five pellets she flew away from the nesting site, probably to collect water. On average females returned after 205 seconds (n = 6) and continued to excavate the entrance of the nest. After 25 to 60 minutes of excavation shafts were sufficiently deep that an excavating female was no longer visible when she had entered the nest. An excavating female now had to back up the shaft with a pellet held between her mandibles. As soon as such a female had left the nest entrance she turned about 90° on her vertical axis and performed a pellet dropping flight as described before. About 60 minutes after initiation of the

Table 3. Pollen composition of provision from nine brood cells from four nests of *Ceramus hispanicus* collected on 26 June, 1998 at Barranco de Zorita (n = 1500 pollen grains/provision).

Cell	Nest 1		Nest 2		Nest 3				Nest 4
	1	2	1	2	1	2	3	4	1
Cistaceae									
<i>Helianthemum</i>	94.3%	97.5%	61.9%	75.9%	97.7%	83.8%	64.8%	61.0%	94.9%
Primulaceae									
<i>Coris</i>	1.2%	1.3%	12.1%	6.1%	1.6%	15.2%	33.8%	34.4%	1.0%
Lamiaceae									
four species	0.7%	0.9%	15.0%	11.8%	0.6%	1.0%	1.0%	2.4%	3.0%
Fabaceae									
<i>Lotus</i>	3.8%	0.3%	9.7%	6.0%				0.7%	0.4%
Convolvulaceae			0.2%	0.1%	0.1%		0.3%	0.5%	0.1%
Crassulaceae								0.8%	0.1%
unknown pollen			1.1%	0.1%			0.1%	0.2%	0.5%
Σ	100%	100%	100%	100%	100%	100%	100%	100%	100%

nest a female started to build a turret. At this stage when she backed up the shaft with a soil pellet held between her mandibles she held on to the ground around the rim of the entrance with her hind legs with her venter positioned outwards (Fig. 7). The wet soil pellet was placed on the rim of the entrance of the shaft and worked with the mouthparts from the inside while it was supported on the outer surface with the mid-legs (Fig. 8). Finally the female entered the shaft again and the whole sequence started anew. On a few

occasions the female curved the metasoma around while placing a pellet so that the pellet was obviously supported on its outer surface by the ventral surface of the tip of the metasoma and the mid-legs. After about 15 minutes (interrupted by water collecting flights) the turret was completed and the female resumed excavating the nest as before (Fig. 6). The turret of nest No. 1 was immediately rebuilt to similar design by the female after it had been experimentally destroyed on 23 June.

The females always entered the nest

Table 4. Pollen composition of gut content of five males and five females of *Ceramus hispanicus* collected at Barranco de Zorita (n = 100–250 pollen grains/individual; dbM No. = serial number in the database of V.Mauss, repeated on the determination labels).

dbM No.	Females					Males				
	1419	1421	1424	1430	1432	1418	1426	1435	1441	1442
Cistaceae										
<i>Helianthemum</i>	23%	97%	18%	65%	69%	74%	27%	40%	52%	56%
Primulaceae										
<i>Coris</i>	7%			5%	25%	1%	2%			
Lamiaceae										
<i>Sideritis</i>	28%	3%	15%	10%	3%	16%	38%	2%	15%	3%
<i>Marrubium</i>	1%						6%		1%	34%
other taxa	26%		56%	18%		2%		56%	29%	4%
Fabaceae										
<i>Lotus</i>	14%			1%						
Asteraceae										
<i>Anthemis</i> -type			5%				18%	1%		
Coniferopsida			4%	1%	2%	4%	7%	1%	2%	2%
unknown pollen	1%		2%		1%	3%	2%		1%	1%

head first. They were able to turn around inside the nest, but during excavation they left the entrance always backwards.

Water collection.—Females alighted frequently at the edge of the little stream or on the damp soil in its immediate vicinity to collect water. They were never observed to settle on the water surface. After landing the females often walked a few steps forward, stopped, extended the glossa and started to take up water, this being accompanied by vigorous pumping movements of the metasoma (Fig. 3). During water-collection females often chose spots on the damp soil or at the edge of the water, which were hidden by vegetation. Females were observed much less frequently at the two ponds and the trough than at the stream. Females visiting the ponds stood on the blades of the rushes during water uptake; at the trough they held on to the vertical walls a short distance above the surface of the water.

Forage plants.—Flower-visiting records for imagines are summarized in Table 2. Males visited the flowers of the Lamiaceae extensively while the observed single visits to *Helianthemum cinereum* and the yellow Asteraceae were very short. The females were observed to visit mainly white flowering Lamiaceae and *Lotus corniculatus*. Three times females were observed to change from one plant taxon to another during a single foraging trip, indicating low flower fidelity. The behavioural pattern exhibited on flowers differed remarkably with the plant taxon. While visiting flowers of Lamiaceae the imagines inserted the mouthparts and the distal parts of the head deeply into the corolla. On one occasion it was seen with certainty that the glossa was extended when the head was removed from the flower, indicating nectar uptake. When females alighted on flowers of *Lotus corniculatus* the alae of the flower were pressed ventro-laterally. Simultaneously, the females performed lateral movements with the gaster and moved the distal parts of the forelegs al-

ternately underneath their body. The foretarsi were brought to the mouthparts a few times during the process, indicating pollen uptake. When on flowers of this plant species, the females were never observed to insert their heads into the corolla base.

The brood cells were provisioned with a firm and relatively dry loaf composed of nectar and pollen. The pollen composition of all provision sampled was remarkably similar. All provision contained high percentages of pollen of *Helianthemum apenninum* and *H. cinereum* (Tab. 3); less important pollen sources though well represented in some brood cells were *Coris monspeliensis*, four different species of Lamiaceae, and *Lotus corniculatus*. Pollen of Convolvulaceae and Crassulaceae occurred in small amounts in some cells. Likewise, the alimentary tract of the imagines contained pollen grains of *Helianthemum*, *Coris*, several species of Lamiaceae, and *Lotus*; pollen of Asteraceae occurred in addition (Tab. 4).

Mating behaviour.—Males were most frequently observed at water. They flew in elliptic flight paths along the stream banks in a slow, constant flight about 0.1 m above the ground. The most striking feature of the flying males was the white coloration of the clypeus and the mandibles, which strongly contrasted with the dark coloration of the body. In addition, the antennae, raised at about 45° to the median axis of the body, showed their conspicuously orange-marked curved distal ends. The patrolling males sometimes interrupted their flight and alighted on sun-exposed stones which were situated 0.1 to 1 m (exceptionally 3 m) away from the stream. On the perch the males maintained a characteristic posture. Antennae and wings were raised at about 45° to the median axis of the body; the head was often slightly raised; and the mandibles were usually closed, although it was observed a few times that the glossa was stretched forward slightly (Fig. 2). Perch-

ing males occasionally rubbed the metasoma ventrally and laterally by alternate movements of the hind-legs, or they groomed the head, the thorax and the antennae by alternate movements of the fore-legs. The frequency of perching and the time spent on a perch decreased during the day. In the morning, males stayed for up to 60 s on a perch whereas males alighted only for a few seconds later in the day. Interactions between males were observed occasionally. Two incidents were observed of two patrolling males rapidly approaching each other, falling to the ground, grappling there for a short time and finally separating and flying away. Flying males were also observed to approach perching males resulting in the departure of the latter from the perch, followed by contact in the air, grappling on the ground, and finally separation.

Copulatory attempts were frequently observed at the edge of the stream. Patrolling males approached females which were on the ground collecting water. Males were often observed to turn away after they had nearly reached the females but before coming into contact with them. However, they also frequently pounced on sitting females, vigorous grappling on the ground following (Fig. 9). Insertion of the male genitalia was observed with certainty on three occasions although it probably occurred more often. On one occasion the male lost its hold on the thorax of the female during insertion and held on to a plant while the female tried to escape. The couple was still connected by the genitalia and remained in this position for a further 180 s (Fig. 10). Often the pairs separated after a short spell (1–5 s) of grappling on the ground but some copulations lasted a few minutes, at most six. Pairs never flew off together during copulation but always separated on the ground before they departed independently.

Males also patrolled along plants in a slow, constant flight. Patrolling males were mainly observed in the afternoon at

patches of *Marrubium supinum* about 50 m away from the nesting aggregation. Between 8h00 and 9h00 on 22 June two searching males were observed; between 14h00 and 16h00 eight records of at least six different patrolling males (marked or collected) were made and five females were observed visiting the flowers. No resightings occurred. Copulations were not observed but twice a male briefly approached and followed a honeybee worker (*Apis mellifera* L.). On 23 June one or several males were repeatedly observed patrolling over the nesting aggregation and the adjacent vegetation at 12h40.

Activity pattern of males and females at water.—The results of the activity measurements are summarized in Figure 13. On both days females collected water after 12h30 more frequently than expected (Chi-Square test; $p \leq 0.001$). In contrast the activity of males and the frequency of copulatory attempts was significantly higher before 12h30 (Chi-Square test; $p \leq 0.001$ and $p \leq 0.01$ respectively) and declined in the afternoon. Males were observed to perch more often in the morning than later in the day but this was only significant on 21 June (Chi square test; $p \leq 0.001$; $p = 0.06$ for 24 June). The first male appeared at the stream at 7h36, the first female at 7h43. Males were not observed after 17h20 whereas females collected water until 18h03.

Associated organisms.—A female of a bee (probably *Lasioglossum* sp., Halictidae) was hiding in cell No. 2 of nest No. 1 on June 26. It escaped during excavation.

DISCUSSION

Nest construction.—All species of *Ceramius* for which nesting is known construct a cylindrical turret surmounting the nest entrance (Gess and Gess 1988, 1992, Mauss 1996a). The presence of a turret-like structure in *C. hispanicus* is therefore considered to be a plesiomorphic trait, although the shape of the turret is strongly derived. The homology of the structures is

supported by their identical position at the nest entrance and the strong similarities in the behaviour of turret-construction (cf. Gess and Gess 1980). A possible function of the three converging processes of the turret of *C. hispanicus* may be to camouflage the nest by disguising the contour of the entrance hole. Thereby the nest is nearly invisible to potential vertebrate predators, made more so by hiding the entrance under leaves.

The burrow of *C. hispanicus* differs from that of *C. tuberculifer* (cf. Giraud 1871, cf. Mauss 1996a) and the majority of the Afrotropical *Ceramius* (Gess and Gess 1986, 1988, 1990, 1992) in that the main shaft is not terminated by a cell, a situation which is probably apomorphic. Within the ground-nesting Masarinae lack of a terminal cell at the end of the main shaft is only known for *Ceramius lichtensteinii* (Klug) (Gess and Gess 1980), *Paragia tricolor* Smith (Houston 1984) and *Jugurtia confusa* Richards (Gess and Gess 1980). A further derived character of the nest of *C. hispanicus* is the absence of secondary shafts which are reported to occur in all ground-nesting Masarinae for which nests with more than one cell have been found (cf. Gess 1996: 66 ff., 1999, Gess et al. 1995, Mauss 1996a). As in members of the Afrotropical species-groups 3 and 6 the main shaft of the nest of *C. hispanicus* is enlarged at or near its base. In the remaining taxa of *Ceramius* the main shaft shows a short bulbous enlargement at mid-length (Gess and Gess 1980, 1986, 1988, 1990, 1992) or is not enlarged (Gess 1999, Mauss 1996a). The "bulb" probably allows the imagines to turn around in the shaft (Gess and Gess 1988). Lack of a defined bulb in *C. hispanicus* and *C. tuberculifer* (Mauss 1996a) may be functionally correlated with the comparatively short length of the main shaft which causes the basal turning area to be situated in a tolerable distance to the entrance.

The dimensions of the burrow of *C. hispanicus* and *C. tuberculifer* (cf. Mauss

1996a) are quite similar, but they differ in that the main shaft normally descends more or less vertically in *C. hispanicus* whereas it descends vertically (Giraud 1871) or obliquely to sub-horizontally (Mauss 1996a) in *C. tuberculifer*. The differences may only be modifications related to the nature of the substrate at the nest site. In contrast to *C. tuberculifer* (Mauss 1996a), the main shaft of the nest of *C. hispanicus* is not terminated by a cell. Within *Ceramius* this condition is merely known from *C. lichtensteinii* (Gess and Gess 1988, Gess 1996, Gess 1999) the only member of species-group 5. The existence of constructed mud-cells (sensu Gess and Gess 1986) which are presumably built within an excavated cell and the sub-horizontal orientation of these cells can be assumed to be plesiomorphic traits of *C. hispanicus* which are adopted from the ground-pattern (sensu Ax 1984: 156) of *Ceramius*. They exist in the majority of species of *Ceramius* and are also present in some *Paragia* (cf. Houston 1984, 1986) and *Jugurtia* (Gess and Gess 1980, Gess 1996: 95).

Digging females of *C. hispanicus* use a clearly defined pellet-dropping area over successive days. A set pellet-dropping area is also used by *C. tuberculifer* (Mauss 1996a), *C. rex* Saussure, *C. metanotalis* Richards, *C. bicolor* (Thunberg), *C. capicola* Brauns and *C. socius* Turner (Gess 1996, Gess and Gess 1980, 1988), whilst females of other *Ceramius*-species spread out the pellets over a larger area (Gess and Gess 1980, 1988). All species of *Ceramius* discard pellets in flight, with the exception of *C. tuberculifer*, the females of which move to the pellet-dropping area on foot (Mauss 1996a). The pellet-dropping area of *C. hispanicus* is situated farther away from the nest entrance than in the remaining five species using a defined pellet-dropping area (cf. Mauss 1996a, cf. Gess and Gess 1980, 1988). *C. hispanicus* utilizes a liquid to soften the soil in nest construction. This liquid is probably water since water is frequently collected by the females. Usage of

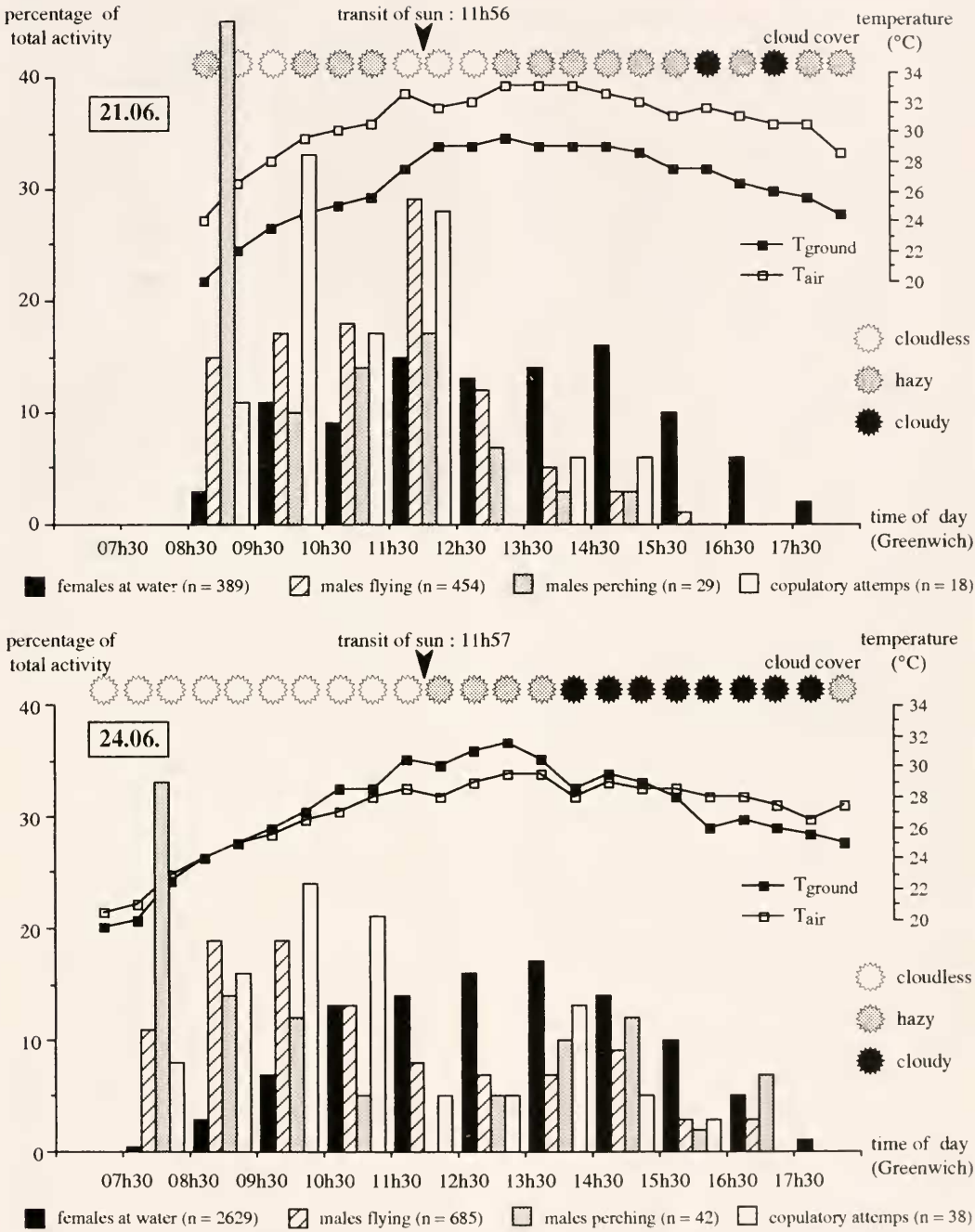


Fig. 13. Activity pattern of males and females of *Ceramius hispanicus* on 21 June and 24 June, 1998 at a little stream in the Barranco de Zorita (prov. Teruel, Spain). The proportion of the summed activity of each hour to the amount of activity of the whole day (= n) is plotted against the time of the day for each category. The line chart shows the temperature changes over the day; covering of clouds is expressed by symbols (for further details see text).

water in nest building has been reported for all Afrotropical *Ceramius* and *C. tuberculifer* (Gess and Gess 1980, 1986, 1988, 1990, Gess 1996, Ferton 1901), although the latter species may use nectar instead (Mauss 1996a). During water collection the females of *C. hispanicus* land on very wet ground or at the edge of a water source. Standing on the ground during water uptake occurs in species-group 2 as well, while members of species-groups 3, 4, 5, and 6 stand on the surface of the water (Brauns 1910, Gess and Gess 1988, 1990, Gess 1996: 76, 1999). Group 8 is exceptional in showing inter- and intraspecific variation in water-collecting behaviour (Gess 1996: 76). Nothing is known about the functional significance of the different water-collecting strategies. The observed vigorous pumping movements of the metasoma of the females during water uptake may serve to eliminate air from the anterior air-sacs to make some space for the dilatation of the crop. However, they may also turn out to be normal respiratory movements after a flight.

Perennial re-use of nests has been recorded for most Afrotropical species which construct mud-cells and *C. tuberculifer* (Gess and Gess 1988, Gess 1996, Mauss 1996a). Reuse of nests by *C. hispanicus* can not be excluded, but it is remarkable that all the nests examined were newly founded. The cell-construction rate of *C. hispanicus* can be roughly estimated from the field data. Based on the present sample, a female starting a new nest can be expected to construct, provision and seal 0.5 (range 0.3 to 0.9) cells per day (open cells were calculated as 0.8 cells). Comparable data are not available for other ground-nesting masarines. The aerial nesting *Celonites abbreviatus* (Villers) was observed also to finish about 0.5 cells per day (calculated from Bellmann 1984).

Forage plants.—*Ceramius hispanicus* is broadly polylectic and capable of dealing with flowers of very different architecture. In the study area the main pollen sources

are *Helianthemum* (Cistaceae) and *Coris* (Primulaceae), to a lesser extent also *Lotus* (Fabaceae) and four species of Lamiaceae. Furthermore, pollen of Crassulaceae and Convolvulaceae is used in small amounts and the occurrence of pollen of Asteraceae in the alimentary tract of males and females indicates that pollen of this family might be used for larval nourishment as well. Flowers of *Helianthemum* exclusively provide pollen (Kugler 1970: 206), so that the females have to take nectar from other plants. Nectar seems to be mainly collected from flowers of various Lamiaceae which is indicated by a high proportion of flower-visiting records being for Lamiaceae despite the comparatively low quantity of pollen of Lamiaceae present in the provisions of the brood cells or in the alimentary tract. Males also consume large amounts of *Helianthemum* pollen indicating that they do not incidentally ingest pollen during nectar uptake but actively feed on it. As already established by Gess & Gess (1988) pollen analysis is the only reliable method to elucidate pollen-plant preferences of masarine wasps.

Some of the remaining members of *Ceramius* species-group 7 are also polylectic. *Ceramius tuberculifer* consumes pollen of Lamiaceae, Cistaceae and Fabaceae (Mauss 1996a) and other members of the *C. lusitanicus*-complex have been recorded visiting flowers of Lamiaceae, Fabaceae and Apiaceae (Richards 1963). The main pollen source of *C. tuberculifer* is *Teucrium montanum* L. (Lamiaceae) and the imagines exhibit behavioural adaptations to the nototribic pollen presentation of Lamiaceae (Mauss 1996a). Such behavioural adaptations seem to be lacking in *C. hispanicus* which uses flowers of Lamiaceae mainly as a nectar source. Afrotropical species of *Ceramius* have not been recorded even as casual visitors of this family (Gess 1989, 1996) with the exception of *Ceramius damarinus* Turner the imagines of which use flowers of Lamiaceae as a nectar source (Gess 1999). It still remains un-

certain whether polylecty is a character of the ground pattern of species-group 7 or if it evolved within the group, as *Ceramius auctus* (F.) which diverged comparatively early may be restricted to Asteraceae (Mauss 1998). In contrast, the Afrotropical species of *Ceramius*, like the majority of the Masarinae (Gess 1996: 46–47), are markedly oligolectic (Gess 1989, 1996: 41) using only pollen of Asteraceae, Aizoaceae or Fabaceae. Furthermore, preferences for single plant families are characteristic at the species-group level in Afrotropical *Ceramius*.

Mating system.—Mate location behaviour of males of *C. hispanicus* includes perching and patrolling at water-collecting sites and also patrolling along flowers of Lamiaceae at times when these are visited by the females. This is confirmed by observations made at Valdelobus (Teruel) where males also patrolled along the edge of a stream and along *Marrubium supinum* (Mauss unpubl.). Multiple encounter sites are common for various aculeate Hymenoptera (Alcock et al. 1978, Eickwort and Ginsberg 1980), however, most cases involve only nesting areas and flowers. *Ceramius* like *Paragia* utilizes three potential encounter sites: nesting areas, flowers and water collecting sites (cf. Gess and Gess 1990, cf. Gess 1996: 59 ff., cf. Houston 1984, cf. Naumann and Cardale 1987). Mate-seeking both at flowers and at water has only been recorded for five Afrotropical species of *Ceramius* (Gess and Gess 1990, Gess 1996: 61, Gess 1999). In *C. hispanicus*, preference for one of the encounter sites seems to be correlated with time of the day. Males are most active at water in the morning, where their activity declines during the day, but they patrol more frequently at flowers in the afternoon. However, total activity of males is much lower at flowers than at water and copulatory attempts were only observed at the latter. Interestingly enough, the males of *C. hispanicus* encountered females at their main nectar sources and not at the

pollen plants. Possibly the probability of a male encountering a female was higher at the nectar-plants, species of Lamiaceae, since these were more aggregated in the study area then were the major pollen-plants which were scattered. Within the patches of Lamiaceae the density of flowers was comparatively high, so that a male could patrol along higher numbers of flowers per unit time than in the more evenly distributed pollen plants, like e.g. *Helianthemum*.

At water, mating occurs more frequently in the morning than in the afternoon which corresponds well with the observation that males appear earlier than females. The decline of male activity in the afternoon is probably not the result of changes of the abiotic conditions, since female activity increases during the day and the fewer males observed still behaved as before. Two reasons should be considered. First, the males may require nectar since they have depleted their energy reserves and secondly, the number of virgin females may decline during the day due to the mating effort of the males. A comparable activity pattern is exhibited by males of the Australian masarine *Paragia tricolor*, which Houston (1984) observed flying around shrubs between 8h30 and 14h00 diminishing in numbers after midday. Males of *C. tuberculifer* were observed to patrol along flowers between 10h30 and 14h00 (Mauss 1996a). At water, the males of *C. hispanicus* alternate between perching and patrolling. The proportion of perching to patrolling is highest at the onset of the daily flight period and declines rapidly thereafter. This may be correlated with rising temperature (cf. Alcock et al. 1978), but as the males are active ahead of the females it could be the arrival of the females which prompts this behavioural change as well. The few incidents of grappling between males indicate that some kind of territoriality is involved in the mating system (cf. Eickwort and Ginsberg 1980). It is important to emphasize that the

males probably did not mistake each other for a female, since all combats started in the air. In contrast, patrolling males were never observed to approach flying females, but frequently pounced on females sitting on the ground. Important visual signals which enable the males to recognize each other possibly come from their distinct coloration of head and antennae. During mating, the males grappled vigorously with the females giving the impression of a forced copulation. This could indicate that the majority of the females had been inseminated already. On the other hand it may be possible that the females test the potential fitness of a male by offering resistance.

Knowledge about the daily period of flight activity of *Ceramius* is very fragmentary. *C. hispanicus* seems to be unusual in that its activity lasts for about 10 hours being from 8h00 to 18h00 and imagines are not much affected by some cloud cover. Females even collected water in the evening after the stream was completely shaded by the ridge of the mountains. In contrast the active period of the Afrotropical species and of *C. tuberculifer* seems to be shorter (Gess and Gess 1980, 1990, Mauss 1996a) and their imagines are very sensitive to less favourable weather conditions in general and disappear quickly when the sun is obscured by cloud or a breeze gets up (Gess and Gess 1980, Mauss 1996a).

Associated organisms.—Presence of female halictine bees in nests of *Ceramius* has also been recorded for *C. lusitanicus* (Klug) (Mauss, unpubl.), the nests of which they were observed to appropriate.

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